

ON THE SYSTEMATIC POSITION OF
MONROIKA AFRICANA (MONRO)
(POLYCHAETA: SABELLIDAE: FABRICIINAE)
AND A DESCRIPTION OF A NEW FABRICIIN
GENUS AND SPECIES FROM AUSTRALIA

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Abstract. — The definition of the monotypic sabellid polychaete genus *Monroika* Hartman is emended based on additions to the description of the type species, *Manayunkia africana* Monro. Although type and nontype material is poorly preserved, the branchial crown appears to have a construction like that of some *Manayunkia* species. A cladistic analysis of fabriciin taxa (sensu Fitzhugh) places *M. africana* either as a sister group to, or as a species within *Manayunkia*. Potential systematic consequences of these results are discussed. A new genus and species from Australia, *Parafabricia ventricingulata*, is described, which is a sister taxon to *Augeneriella* Banse and *Fabricinuda* Fitzhugh.

The sabellid polychaete *Manayunkia africana* Monro, 1939 is a small, tubicolous, freshwater species known only from Matadi, Democratic Republic of the Congo, approximately 150 km upstream from the mouth of the Congo River. The species is described by Monro (1939:220) as living in swift water, forming "... incrustations composed of clusters of small intertwining sandy tubules" on the shells of the freshwater gastropod, *Hydrobia plena*, as well as on stones. Whereas Monro apparently examined specimens only found on *H. plena*, he attributed to *M. africana* some dried tubes encrusted on a stone from the M'Pozo River, upriver from Matadi.

Monro's placement of this polychaete species in *Manayunkia* rested on the reported presence of near-"spatulate" thoracic notosetae (=pseudospatulate setae sensu Fitzhugh 1989, see below) in some other species of *Manayunkia*. *Manayunkia africana* is said to have "spatulate" setae in setigers 2–5. Monro did not comment on the rarely described (e.g., Zenkevitch 1925: fig. Gh, i) occurrence of this setal form in

Fabricia stellaris [Müller; =*F. sabella* (Ehrenberg), see Fitzhugh 1990d].

Monro (1939:220) reported that the state of preservation of specimens is poor, such that "delicate parts such as the gills are partly disintegrated." Thus, his illustration (Monro 1939:fig. 1) of the branchial crown is not very informative. Monro did, however, describe the branchial crown as being composed of about 12 "filaments" (=radioles), lacking "barbules" (=pinnules), which are joined by a "high palmer membrane." The opinion that the branchial crown of *Manayunkia* species lacks pinnules (= "barbules") has been a common misconception (e.g., Southern 1921, Friedrich 1939, Hartman 1951; but see, however, Zenkevitch 1925, Pettibone 1953:fig. 1C, D).

In a review of fabriciin taxa (sensu Rioja 1923), Hartman (1951) proposed the new genus *Monroika* to accommodate *Manayunkia africana*. Hartman's basis for this change rested solely on Monro's (1939) description of the putative unique combination of numerous nonpinnulate radioles and

a palmate membrane. Hartman thus considered *Monroika* similar to *Manayunkia* on the common (though erroneous) assumption that all species in both genera have nonpinnulate radioles (see below).

The most thorough description of *Monroika africana* is given by Jones (1974) based on the type material. While Jones provided excellent illustrations of all setal forms, drawings of the body (Jones 1974:fig. 1) are incomplete insofar as the branchial crown is not shown and is not described. While Jones (1974:219) supported Hartman's (1951) decision to erect *Monroika*, he considered the "type and distribution of setae and the number of thoracic and abdominal setigers" to be the "crucial generic differences between *Monroika* and *Manayunkia* . . ." as opposed to the questionable presence of a palmate membrane.

This paper is a partial emendation of the definition of *Monroika* based on type and nontype material of *Manayunkia africana*. A new fabriciin (sensu Fitzhugh 1989, 1991a) genus and species from Australia, *Parafabricia ventricingulata*, is also described. The cladistic relationships and status of *Monroika* and *Parafabricia* are then examined in relation to other fabriciin genera and species. Morphological terms used here follow from definitions given by Fitzhugh (1989) and their subsequent application by Fitzhugh (1990a, 1990b, 1990c, 1990d, 1990e, 1991a).

Specimens examined are deposited in one of the following institutions: Allan Hancock Foundation Collection of the Los Angeles County Museum of Natural History (LACM-AHF), British Natural History Museum (BMNH), U.S. National Museum of Natural History, Smithsonian Institution (USNM), and the Australian Museum, Sydney (AM).

Monroika Hartman, 1951, emended

Monroika Hartman, 1951:389; 1959:551 [list].—Jones, 1974:218–219.—Fau-chald, 1977:139.

Type species.—*Manayunkia africana* Monro, 1939, by monotypy.

Diagnosis.—Fabriciin species with 8 thoracic and 2 abdominal setigers. Branchial crown with 2 pairs of radioles; all pinnules arranged in pectinate fashion except for unpaired proximalmost pinnule of first radiole being displaced and adjacent to dorsal lips. Dorsal lips erect, broadly rounded. Presence or absence of ventral lips unknown. Pair of vascularized, filamentous appendages present. Branchial hearts (?) poorly developed. Branchial lobes not fused middorsally. Branchial skeleton absent. Anterior peristomial ring developed as a membranous collar; narrowly separated middorsally. Posterior peristomial ring collar absent. Peristomial and pygidial eyes absent. Superior thoracic notosetae elongate, narrowly hooded. Inferior thoracic notosetae of setigers 1–2 and 6–8 short forms of elongate, narrowly hooded; setigers 3–5 pseudospatulate. Thoracic uncini acicular; large tooth above main fang; hood present. Abdominal uncini rasp-shaped plates; manubrium about same length as dentate region; dentate region with several teeth per row. Abdominal neurosetae modified, elongate narrowly hooded.

Remarks.—The present diagnosis is consistent with that given by Jones (1974) except that the distribution of pseudospatulate setae is limited to setigers 3–5 as opposed to 2–5. While inferior thoracic notosetae in setiger 2 are short forms of the elongate, narrowly hooded condition of superior thoracic notosetae, the former are slightly shorter than the inferior thoracic notosetae in setigers 6–8 and the proximal region of the hood is slightly wider. As a result, inferior thoracic notosetae of setiger 2 can have an almost intermediate appearance to inferior elongate, narrowly hooded and pseudospatulate forms. A similar phenomenon has been noted by Banse (1956) in species of *Fabricia* Blainville, 1828.

The branchial crown appears to show a pattern of construction identical to that of

several *Manayunkia* species, e.g., *M. speciosa* Leidy, 1859 and *M. baicalensis* (Nusbaum, 1901), in that pinnules extend from the radioles in a pectinate arrangement (see cladistic analysis below; Fig. 4A). In addition to there being only two pairs of radioles, a pair of dorsal lips, and a pair of vascularized, ventral filamentous appendages, there also are a pair of slender, unbranched appendages just dorsal to the dorsalmost radioles and which are continuous with the dorsal lips (cf. Fig. 4A, B). These appendages are referred to here as displaced pinnules and are the same as what Zenkevitch (1925:fig. D) called dorsal lips (*Dorsallippenauswüchse*) in *M. baicalensis* and what Pettibone (1953:fig. 1D) referred to as mediiodorsal tentacles in *M. speciosa*. Banse (1956:425–426) suggested these appendages in *Manayunkia* are homologous to pinnules of the dorsalmost radioles, having migrated to a more proximal position on the radiole. Fitzhugh (1989:63) noted, however, that in *M. speciosa* the side from which pinnules extend from the dorsalmost radioles is ventral to this structure (Fig. 4A). Additional aspects of the displaced pinnules in *Manayunkia* and *Monroika* are discussed in the cladistic analysis below.

Monroika africana (Monro, 1939)

Manayunkia africana Monro, 1939:220–223, figs. 1–5.—Wesenberg-Lund, 1958:29 [list].

Monroika africana.—Hartman, 1951:389–390; 1959:551 [list].—Jones, 1974:219–221, figs. 1, 2, table 1.—Fauchald, 1977:139 [list].

Material examined.—Democratic Republic of the Congo, Congo River at Matadi, E. Darteville, coll. Syntypes: 1 incomplete specimen mounted on microscope slide (BMNH 1939.7.17.1); 3 incomplete specimens mounted on microscope slide (BMNH 1939.7.17.2). Additional material: several incomplete specimens mounted on slide (USNM 50913); several complete speci-

mens from sandy tubes on two *Hydrobia plena* shells (BMNH ZK 1939.7.17.13–14).

Description.—All specimens in very poor, degraded condition. Branchial crown comprising about one-fifth of total body length. Two pairs of radioles, each with 3–5 pairs of pinnules; all pinnules terminate at about same height. A pair of displaced pinnules present between dorsal midline and dorsalmost radiole pair; terminate at same height as pinnules. Displaced pinnules lead to pair of low dorsal lips. Vascularized ventral filamentous appendages present, same height as radioles. Branchial hearts present, poorly developed. Membranous, anterior peristomial ring collar highest ventrally, broadly rounded; very shallow laterally then slightly higher dorsolaterally; dorsolateral margins with pair of narrow, shallow notches; completely separated middorsally by narrow gap. Demarcation between anterior and posterior peristomial rings not visible. Tubes about 2 times longer than animals, composed of quartz sand grains and some detritus; very firm. No brooding observed.

Remarks.—Setal counts can be found in Jones (1974:tables 1, 2), with the exception that what he described as “spatulate” setae in setiger 2 are here called short forms of elongate, narrowly hooded setae (see Remarks above). All features described here are illustrated by Jones with the exception of the branchial crown.

Discerning specific structures on the branchial crown is extremely difficult. For example, establishing the pattern of pinnule branching, the presence of displaced pinnules, and presence of ventral filamentous appendages is only possible by way of tracing what appear to be blood vessels and musculature. As a result, I am not wholly confident of my interpretation of branchial crown structures. Some implications of these limitations are discussed below as part of the cladistic analysis.

Parafabricia, new genus

Type species.—*Parafabricia ventricingulata*, new species.

Etymology. — The genus name is derived from its inferred close relationship and appearance to *Fabricia*.

Diagnosis. — Fabriciian species with 8 thoracic and 3 abdominal setigers. Branchial crown with 3 pairs of radioles, pinnules arranged in pectinate fashion. Dorsal lips triangular. Ventral lips and ventral filamentous appendages absent. Branchial hearts present. Branchial lobes not fused middorsally. Branchial skeleton absent. Anterior peristomial ring margin developed ventrally as broad, distally rounded lobe, laterally and dorsally as rounded shelf; dorsolateral, lateral and portion of ventral areas of ring concealed by posterior peristomial ring. Posterior peristomial ring distinctly wider than long. Posterior peristomial ring collar absent. Peristomial and pygidial eyes present. Transverse “glandular” ridge present on ventrum of setiger 5. Superior thoracic notosetae elongate, narrowly hooded. Inferior thoracic notosetae of setigers 2 and 8 short forms of elongate, narrowly hooded state; setigers 3–7 pseudospatulate. Thoracic uncini acicular; large tooth above main fang; hood present. Abdominal uncini rasp-shaped plates; manubrium about same length as dentate region; dentate region with several teeth per row. Abdominal neurosetae modified, elongate narrowly hooded. Body wall pigmentation usually restricted to branchial crown and thoracic region; light to dark brown; well to poorly developed.

Remarks. — *Parafabricia* is the sister group to *Augeneriella* Banse, 1957 and *Fabricinuda* Fitzhugh, 1990c (see cladistic analysis below); the sister group to this clade is *Fabricia*. *Parafabricia* closely resembles both *Fabricia* and *Augeneriella* in development of the ventral lobe of the anterior peristomial ring and the distribution of thoracic inferior pseudospatulate setae in setigers 3–7. The short manubrium state in abdominal uncini distinguishes *Parafabricia* from *Fabricia* (see also Banse 1956; Fitzhugh 1989, 1990d), whereas *Augeneriella* has branched, vascularized, ventral filamentous appendages. *Fabricinuda* has pseudospatulate setae

in setigers 3–8 and lacks the ventral lobe extension of the anterior peristomial ring.

The most distinctive features of *Parafabricia* include 1) partial extension of the posterior peristomial ring segment over the anterior ring, resulting in an obvious mid-dorsal gap in the posterior ring, and 2) the ventral “glandular” ridge on setiger 5. This ridge closely resembles the “glandular girdle” encircling setiger 2 of some plesiomorphic sabellin genera (sensu Fitzhugh 1989, 1991a), e.g., *Desdemona* Banse, *Oriopsis* Caullery & Mesnil, *Chone* Krøyer, and *Jasmineira* Langerhans. Aspects of this ridge are discussed below in the Remarks on *P. ventricingulata*.

Parafabricia ventricingulata, new species

Figs. 1–3

Material examined. — Australia, Queensland, Great Barrier Reef, upper reef crest on northeastern side of One Tree Reef, 23°30'S, 152°05'E, in intertidal mats of green alga *Boodlia composita*, 6 Dec 1987, coll. G. Rouse. Holotype (AM W 20717). Paratypes (in alcohol): 2 complete specimens (AM W 20718), 1 complete specimen (LACM-AHF 1536), 1 complete specimen (USNM 142107). Paratypes (embedded in Spurr's resin), same locality, June 1987, coll. G. Rouse: 1 block with 2 incomplete specimens (AM W 20719), 2 blocks each with 2 incomplete specimens (LACM-AHF 1537, 1538), 1 incomplete specimen (USNM 142108). Paratype (embedded in Spurr's resin), same locality, collected late 1988, coll. G. Rouse: 1 block with 2 incomplete specimens (AM W 20720).

Description. — Holotype complete with 8 thoracic and 3 abdominal setigers. Total body length 2.0 mm; branchial crown comprising 0.5 mm of this length; maximum width about 0.3 mm. Body cylindrical, short; widest at midthorax with slight tapering anteriorly and posteriorly (Fig. 3A). Distal ends of radioles filamentous, about same width as pinnules. Five to 7 pairs of pinnules per radiole; all terminating at about same height as radioles. Dorsalmost pair of radioles of

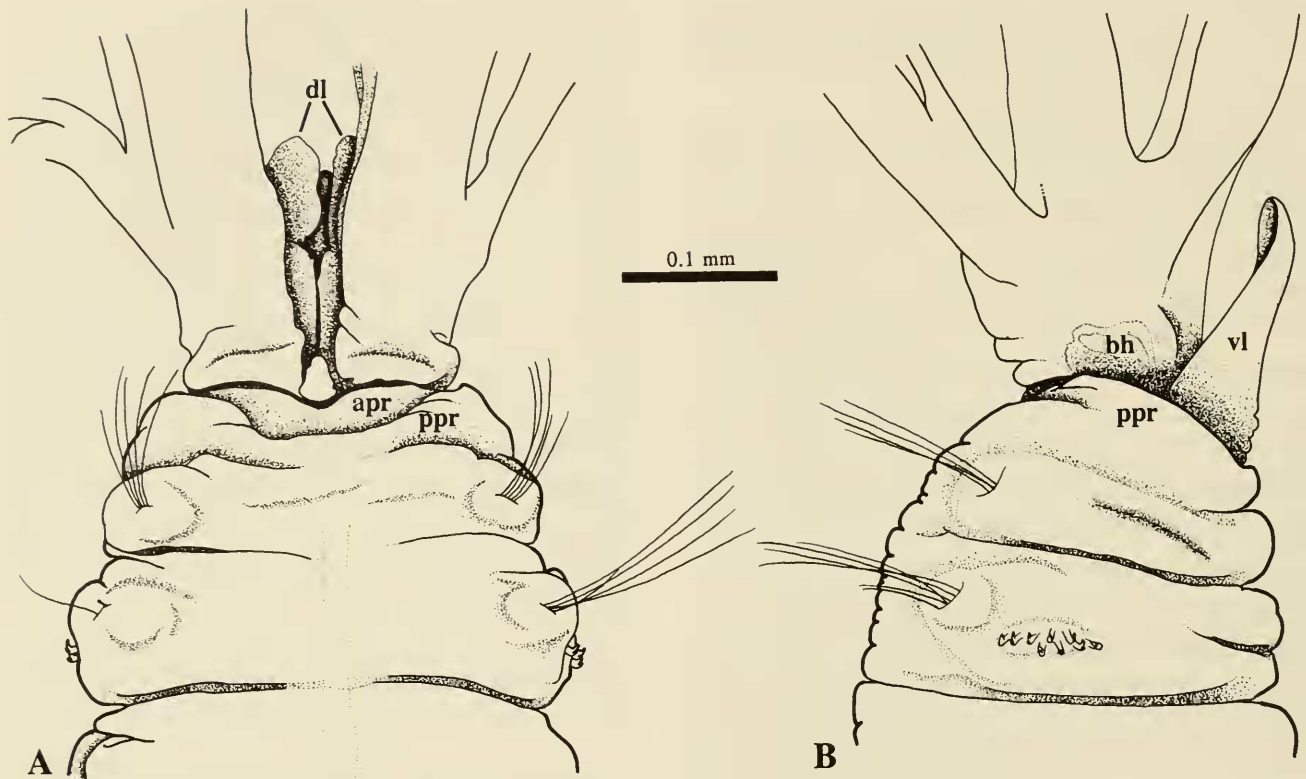


Fig. 1. *Parafabricia ventricingulata* (Paratype, AM W 20718). A, B, Dorsal and lateral (right side) views of anterior end, respectively. Abbreviations: apr—anterior peristomial ring; bh—branchial heart; dl—dorsal lips; ppr—posterior peristomial ring; vl—ventral lobe extension of anterior peristomial ring.

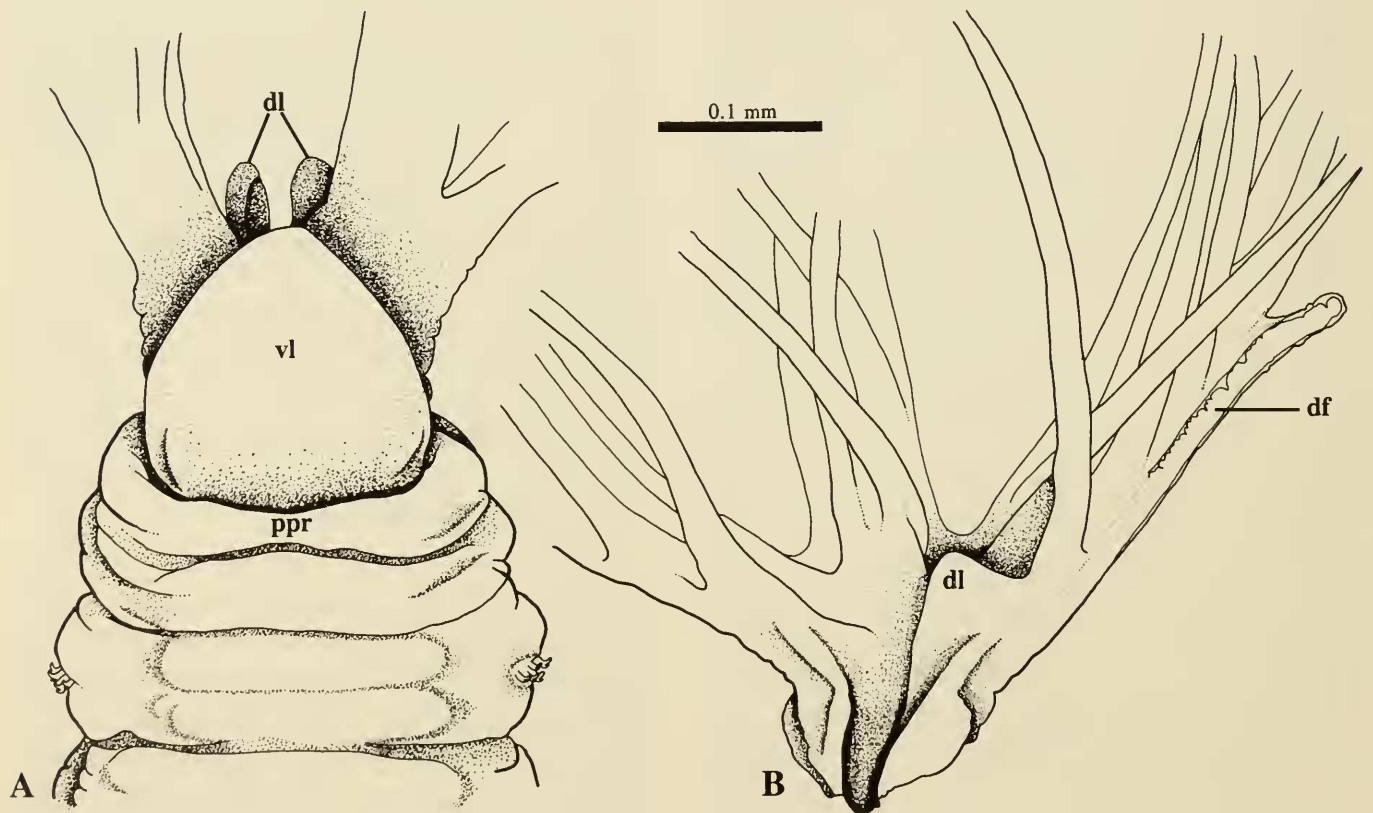


Fig. 2. *Parafabricia ventricingulata* (Paratypes, AM W 20718). A, Anterior end, ventral view; B, Right half of branchial crown, inner view. Abbreviations: df—filamentous appendage on dorsalmost radiole; dl—dorsal lips; ppr—posterior peristomial ring; vl—ventral lobe extension of anterior peristomial ring.

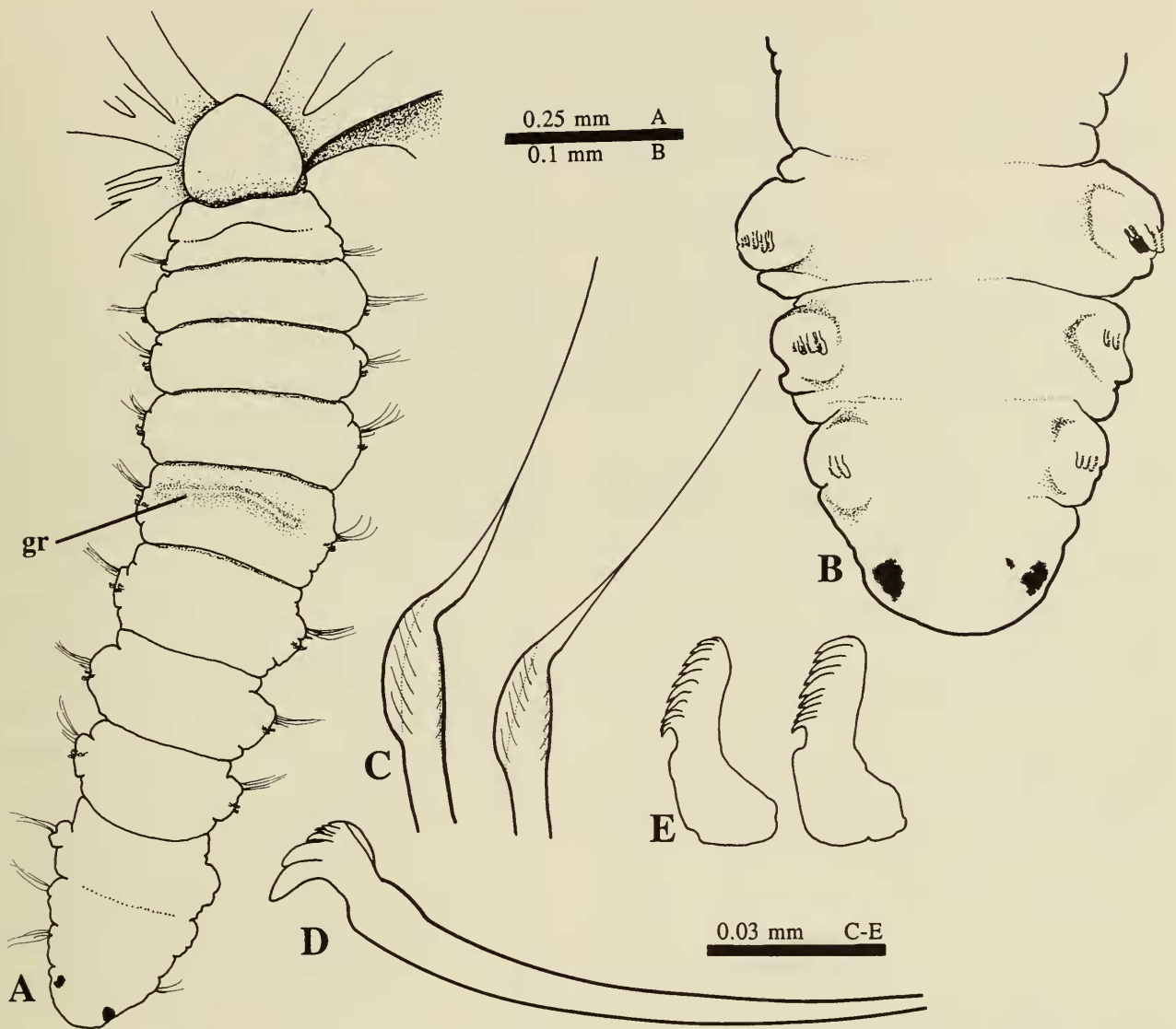


Fig. 3. *Parafabricia ventricingulata* (Paratypes, AM W 20718). A, Ventral view of thoracic and abdominal regions; B, Posterior end, dorsal view; C, Thoracic notosetal pseudospatulate setae from setiger 4; D, Thoracic uncinus from setiger 5; E, Abdominal uncini from setiger 9. Abbreviations: gr—"glandular" ridge on setiger 5.

large animals (>2.0 mm total length) each with an unbranched, vascularized filament extending from radiole margin closest to dorsal midline of body (Fig. 2B); free end of filaments short, distally blunt, about same width as radioles; large blood vessel in filament continues proximally into radiole, giving appearance of filament being fused to radiole margin for most of length. Dorsal lips erect, triangular, distally rounded (Figs. 1A, 2). Anterior margin of anterior peristomial ring only visible middorsally as low shelf (Fig. 1A); ventrally as broad, thin lobe, widest proximally, broadly rounded distally, about 2.0–2.5 times longer than posterior

peristomial ring (Figs. 1B, 2A, 3A). Posterior peristomial ring with slightly inflated appearance dorsolaterally, laterally, and ventrally, extending over and covering anterior ring dorsolaterally and laterally, lowest middorsally to form wide gap (Fig. 1A). Annulation between anterior and posterior peristomial rings only visible middorsally and ventrally. Pair of peristomial eyes in anterior or posterior peristomial ring, round, deeply set within body and indistinct. Pygidial eyes round, usually with irregular borders, black (Fig. 3A, B). Low, transverse "glandular" ridge on ventral anterior half of setiger 5 (Fig. 3A), very distinct in ani-

mals with surrounding pigmentation, ridge unpigmented, white to cream colored. Anterior peristomial ring (exclusive of ventral lobe) about same length as posterior ring. Setiger 1 about same length as, or slightly longer than, posterior peristomial ring (Fig. 3A); setigers 2–4 each about same length as setiger 1 or each successively longer; setigers 5–8 each about same length as setiger 4 or slightly longer. Setiger 9 about same length as setiger 8, setigers 9–10 each successively shorter. Pygidium about same length as setiger 11, very broadly rounded posteriorly (Fig. 3A, B). Superior thoracic notosetae elongate, narrowly hooded; 4–5 per fascicle. Inferior thoracic notosetae of setigers 2 and 8 short, elongate, narrowly hooded; 2–3 per fascicle; setigers 3–7 each with 2 pseudospatulate setae with very long, drawn out tips (Fig. 3C). Abdominal neurosetae modified, elongate, narrowly hooded; 3–5 per fascicle. Five to 9 thoracic acicular uncini per fascicle (Fig. 3D), forming two slightly staggered rows. Abdominal uncini as rasp-shaped plates (Fig. 3E); 10–11 rows of teeth in profile, 4–6 teeth per row; manubrium about same length as dentate region, constricted distally and slightly expanded proximally; 12–17 uncini per fascicle. Large individuals usually with dark brown pigmentation on branchial lobes just dorsal to dorsal lips, proximal regions of radioles light brown; crown of small individuals usually cream colored or only lightly pigmented. Anterior and posterior peristomial rings and anterior thoracic setigers light to dark brown, fading in posterior setigers with abdomen and pygidium cream colored. Tubes fragile, composed of fine white coral sediment and mucus (G. Rouse, pers. comm.).

Etymology.—The specific epithet refers to the ventral “glandular” ridge on setiger 5.

Remarks.—The “glandular” ridge in *P. ventricingulata* is most prominent in specimens with pigmentation extending back through this region since the ridge itself is not pigmented. Because pigmentation is not as extensive in smaller individuals, the ridge

is usually not visible, and in larger specimens lacking pigment in setiger 5, the ridge is very indistinct even with methyl green staining since the ridge does not take up stain and the surrounding area only stains lightly. In some stained specimens, ventral intrasegmental grooves in anterior thoracic setigers (e.g., Fig. 2A) will not stain, thus mimicking the condition seen in setiger 5.

Based on available material, the odd filamentous structures extending from the dorsalmost radioles (Fig. 2B) do not develop until the specimens reach a minimum total length of about 2.0 mm. Intermediate growth conditions of this filament are absent in smaller individuals and there is no evidence of the structure within the radiole. A similar structure is described by Fitzhugh (1990a:10, fig. 6A) from the second pair of radioles of *Novafabricia chilensis* (Hartmann-Schröder). In this latter instance, however, Fitzhugh interpreted this filament as a proximalmost pinnule. The filaments in *P. ventricingulata* do not appear to be pinnules since all pinnules form paired groups and the former structure arises after the proximal pinnules have formed.

Systematic Relationships of *Monroika* and *Parafabricia* to other Fabriciinae Taxa Figs. 4–8; Tables 1, 2

The positions of *Monroika* and *Parafabricia* within the Fabriciinae were determined from a cladistic analysis involving 36 species and 21 characters. Outgroup considerations follow from the analyses carried out by Fitzhugh (1991a).

New characters and states.—Twenty-one characters, totaling 40 apomorphic states, were used in the present analysis (Table 1). Most characters and states used here have been described and applied by Fitzhugh (1989, 1990a, 1990b, 1990c, 1990d, 1990e, 1991a, 1991b). Modifications of one of these characters and the introduction of three new characters are discussed here.

Development of the breast into a ma-

Table 1.—Characters and states used to determine cladistic relationships of *Monroika africana* and *Parafabricia ventricingulata* to other fabriciina taxa. State “0” is plesiomorphic based on outgroup comparisons (see text). Order of multistate characters does not imply any views on transformation series

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1. Ventral filamentous appendages: (0) absent; (1) nonvascularized, unbranched; (2) vascularized, unbranched; (3) vascularized, branched.
 2. Dorsal lips: (0) well-developed, triangular lobe; (1) low narrow ridge; (2) absent.
 3. Position of branchial crown: (0) extends over entire anterior end; (1) shifted dorsally somewhat; (2) extensively shifted dorsally.
 4. Branchial lobe shape: (0) wide and short; (1) narrow and elongate and/or with a peduncle-like process.
 5. Anterior margin of anterior peristomial ring: (0) low ridge dorsally and laterally, ventrally as a narrow lobe; (1) low membranous collar; (2) membranous collar low dorsally and laterally, higher ventrally; (3) very high membranous collar; (4) low ridge dorsally and laterally, ventrally as a broad lobe; (5) low ridge dorsally and laterally, ventrally as a tongue-like lobe; (6) low ridge all around; (7) low ridge all around except for dorsolateral lobes.
 6. Middorsal collar condition: (0) separate; (1) entire and distinctly grooved; (2) entire and surface smooth.
 7. Dorsolateral incisions on anterior margin of anterior peristomial ring collar: (0) absent; (1) present.
 8. Anterior peristomial ring dimensions: (0) wider than long; (1) at least as long as wide.
 9. Peristomial eyes in lateral view: (0) well developed and round; (1) poorly developed and crescentic; (2) absent.
 10. Distribution of inferior thoracic pseudospatulate notosetae, in setigers 2–8: (0) absent; (1) 2–5; (2) 3–5; (3) 3–6; (4) 3–7; (5) 3–8; (6) broadly hooded, flagellate in 3–7.
 11. Thoracic uncini: (0) without large tooth above main fang; (1) large tooth above main fang.
 12. Thoracic uncini main fang: (0) slender; (1) swollen.
 13. Abdominal uncini teeth: (0) > 1 row of teeth; (1) 1 row of teeth.
 14. Abdominal uncini breast: (0) oriopsis-like; (1) manubrium about 2.0 times longer than dentate region; (2) manubrium about 1.5 times longer than dentate region; (3) manubrium same length as dentate region.
 15. Pygidial eyes: (0) absent; (1) present.
 16. Radioles: (0) 3 or more pairs; (1) 2 pairs.
 17. Body wall spicules: (0) absent; (1) present.
 18. Branchial hearts: (0) absent; (1) present.
 19. Displaced pinnules (e.g., *Manayunkia*, *Monroika*): (0) absent; (1) present.
 20. Thoracic uncini shape: (0) typical fabriciina shape; (1) *Manayunkia*/Genus A-type.
 21. Pinnule arrangement: (0) distinctly pectinate; reduced to two (1) to four (2) pinnules at bases of branchial lobes.
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nubrium in abdominal uncini of Fabriciinae (character 14) has usually been separated into two states (e.g., Fitzhugh 1991a, 1991b): the manubrium being longer than the dentate region or about the same length as the dentate region. This character is now interpreted as comprising three apomorphic states: manubrium about two times longer than the dentate region (state 1), manubrium about 1.5 times longer than the dentate region (2), and manubrium about the same length as the dentate region (3).

The pair of displaced pinnules (character 19) originating just dorsal to the first pair of radioles are discussed under the Remarks on *Monroika*; these appendages being a fea-

ture also occurring in some species of *Manayunkia* (Fig. 4A, B; see also the “mediodorsal tentacles” in Pettibone 1953:fig. 1D). The most pressing issue at this time is whether or not these displaced pinnules are homologous to the dorsalmost pinnules in species of *Manayunkia* in which the radioles are supposedly reduced and the pinnules arise directly from the branchial lobes [e.g., *M. aestuarina* (Bourne, 1883), *M. polaris* Zenkevitch, 1935; Fig. 4C] as opposed to the more typical pectinate arrangement of pinnules along the radioles (e.g., *M. speciosa*, *M. baicalensis*).

For example, in some *Manayunkia* species, such as *M. aestuarina* and *M. polaris*

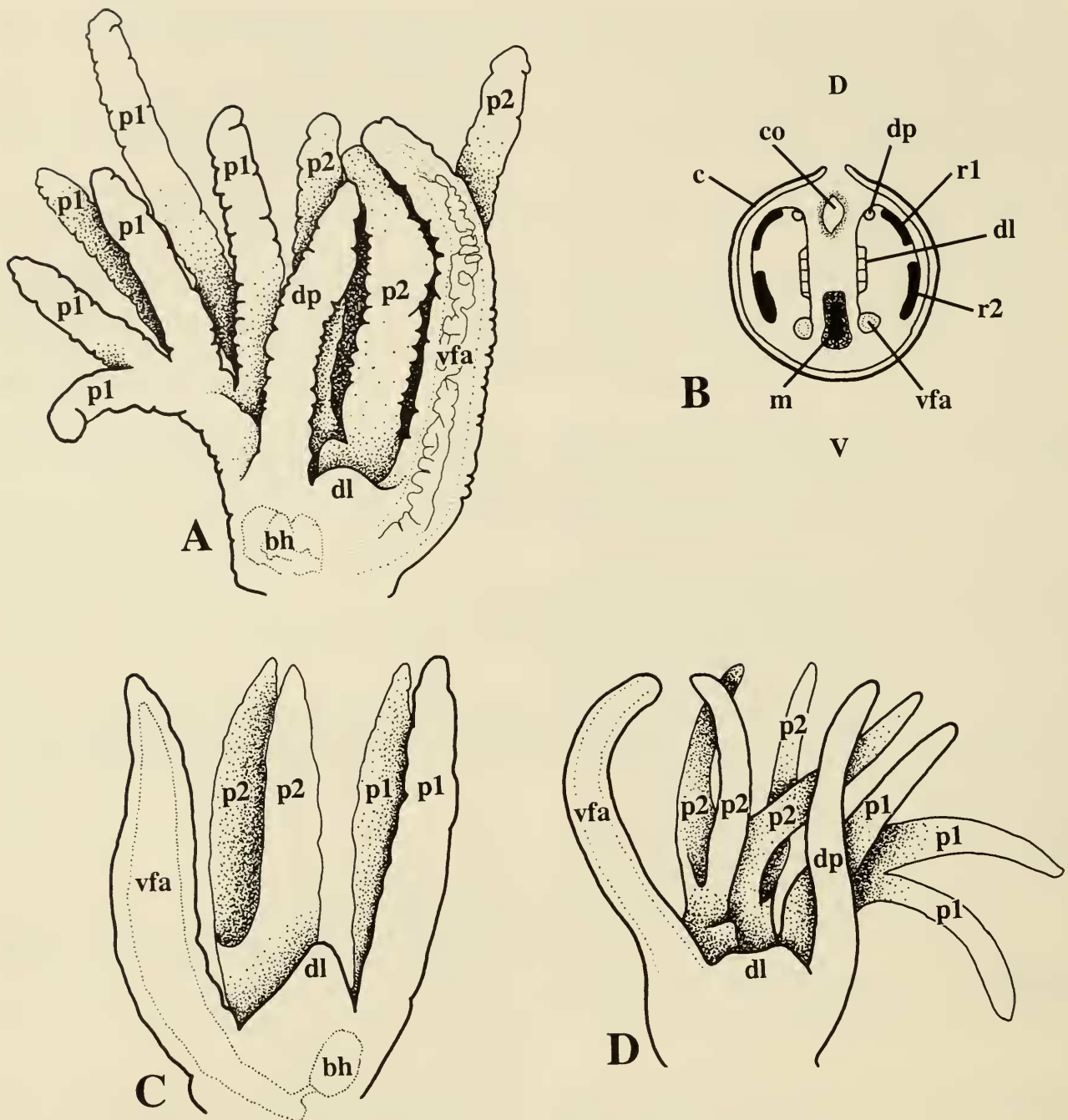


Fig. 4. Branchial crown structures of representative *Manayunkia* species. All radiolar appendages are interpreted as pinnules (see text for explanation). A, Left half (inner margin) of branchial crown of *Manayunkia speciosa* Leidy (LACM-AHF 3432). B, Schematic arrangement (adapted from Banse 1956:fig. 6.2b₂) of anterior thoracic and branchial crown structures of *M. speciosa*. C, D, Right half of branchial crown (inner margin) of *M. aestuarina* (Bourne; modified from Banse 1956:fig. 6.1b₁) and *M. brasiliensis* (modified from Banse 1956: fig. 4a), respectively. Abbreviations: bh—branchial heart; c—anterior peristomial ring collar; co—cone-like structure; D—dorsal margin; dl—dorsal lip; dp—displaced pinnule; m—mouth; r1—dorsalmost radiole; r2—ventralmost radiole; p1—pinnule of dorsalmost radiole; p2—pinnule of ventralmost radiole; V—ventral margin; vfa—vascularized, ventral filamentous appendage.

(Zenkevitch 1935:196, fig. 3), the dorsalmost pinnules in each half of the branchial crown (Fig. 4C) arise adjacent to the dorsal lips as seen in displaced pinnules. Displaced pinnules also appear to occur in *M. brasiliensis*

brasiliensis Banse, 1956 (Fig. 4D), a species with a branchial crown construction intermediate to that of *M. speciosa* and *M. aestuarina*.

Whereas displaced pinnules clearly occur in some *Manayunkia* species (e.g., Fig. 4A,

B, D) and appear to be in *Monroika africana*, a more fundamental problem centers on 1) the relationship of these pinnules to the putative pinnules in species like *M. aestuarina* (Fig. 4C) and *M. polaris*, 2) the presence of paired as opposed to unpaired pinnules, and 3) the presence or absence of distal filamentous radiolar ends.

The most common condition in sabellid radioles is where the distal end of a radiole terminates to a slender filament (e.g., Perkins 1984:fig. 4A; Fitzhugh 1989:figs. 12B, C, 13C). Typically, pinnules are arranged in a paired series along most of the radiole length, with pinnules of a pair lying slightly oblique to one another. Unpaired pinnules can be found in the dorsalmost radiole of each half of the branchial crown of some sabellin species, with one or several of these (unpaired) pinnules enlarged and/or fused to the dorsal lips (Orrhage 1980; = dorsal pinnular appendages sensu Perkins 1984, Fitzhugh 1989).

By extension, if displaced pinnules in *Manayunkia* species are viewed as being unpaired within a radiole, then the dorsalmost radiole of *M. speciosa* in Fig. 4A has one unpaired pinnule (the displaced pinnule) and three groups of paired pinnules but with no distal filamentous end to the radiole. Conversely, if the filamentous radiole end is considered present, there are three pairs of pinnules, with the displaced pinnule a member of the proximalmost pinnule pair. *Manayunkia brasiliensis* (Fig. 4D) then has either one unpaired pinnule and one group of paired pinnules and a long filamentous end to the radiole or else lacks the filamentous radiole end and has two pairs of pinnules. Similar interpretations can be applied to *M. aestuarina*, with the implication that either a single pinnule and filamentous radiole are present or there are only a pair of pinnules (Fig. 4C). In either case, if the strict criterion of position is applied, then the dorsalmost pinnule in *M. aestuarina* is homologous to a displaced pinnule, though the state of being displaced is really

not evident. Since such a relationship has yet to be determined, I am taking a conservative approach and assume that species such as *M. aestuarina* and *M. polaris* have reduced radioles, each represented by one pair of pinnules (Fig. 4C) and that the dorsalmost pinnules are not displaced.

The arrangement of pinnules (character 21) can be distinguished as arising in a pectinate pattern (state 0; Fig. 4A) as opposed to the extremely reduced condition (state 1; Fig. 4C) typical of *M. aestuarina* and *M. polaris*, or an intermediate condition (state 2; Fig. 4D) seen in *M. brasiliensis*.

The general shape of the distal ends of thoracic uncini (character 20) within the Fabriciinae can be of two forms. In the plesiomorphic state (0), also seen in plesiomorphic Sabellinae taxa, teeth above the main fang are not very numerous and do not form a dense, crowded group above the main fang (see, e.g., Rouse 1990:figs. 1g, 3f, 4f). In the apomorphic condition (state 1), seen in species of Genus A (Fitzhugh 1989, including *Augeneriella dubia* Hartmann-Schröder, 1965) and *Manayunkia*, teeth above the main fang are very small, numerous and crowded together to give the entire distal ends of uncini a very distinctive profile. This condition is clearly shown in SEM micrographs of *A. cf. dubia* by Rouse (1990:fig. 6f, g). Unfortunately, this state has not been accurately illustrated for *A. dubia* (e.g., Hartmann-Schröder 1965:fig. 85) or *Manayunkia* species (e.g., Bourne 1883:plate IX, figs. 10, 11; Zenkevitch 1925:fig. Ge, 1935:fig. 5d; Annenkova 1928:plate IV, fig. 11; Banse 1956:fig. 4f; Light 1969:fig. 1; Hutchings et al. 1981:fig. 1d).

Taxa included in the analysis.—Thirty-six species from among 10 genera were included in the analysis (Table 2). Most of these species are the same as those used in the analysis performed by Fitzhugh (1991a). Exceptions include the addition of *Monroika africana* and *Parafabricia ventricingulata*, and four species based on work by Fitzhugh (1991b): *Pseudofabriciola capensis*

Table 2.—Character-state matrix for 36 fabriciine species based on character states presented in Table 1.

Species	Characters and states																				
	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18	19	20	21
Outgroup	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
<i>Manayunkia speciosa</i>	2	0	0	0	2	0	0	0	0	0	0	0	0	1	0	1	0	1	1	1	0
<i>M. baicalensis</i>	2	0	0	0	2	0	0	0	0	0	0	0	0	1	0	1	0	1	1	1	0
<i>M. aestuarina</i>	2	0	0	0	2	0	0	0	0	1	0	0	0	1	0	1	0	1	0	1	1
<i>M. brasiliensis</i>	2	0	0	0	2	0	0	0	0	1	0	0	0	1	0	1	0	1	1	1	2
<i>M. polaris</i>	2	0	0	0	2	0	0	0	0	3	0	0	0	1	0	1	0	1	0	1	1
<i>Monroika africana</i>	2	0	0	0	2	0	0	0	2	2	1	0	0	3	0	1	0	1	1	0	0
<i>Augeneriella dubia</i>	2	0	0	0	4	0	0	0	2	0	0	0	0	1	0	0	1	1	0	1	0
Genus A	2	0	0	0	4	0	0	0	2	0	0	0	0	1	0	0	1	1	0	1	0
<i>Fabriciola baltica</i>	1	0	0	0	2	0	0	0	0	0	0	0	0	1	1	0	0	1	0	0	0
<i>F. berkeleyi</i>	1	0	0	0	1	0	0	0	0	0	0	0	0	1	1	0	0	1	0	0	0
<i>F. ghardaqa</i>	1	0	0	0	1	0	0	0	0	0	0	0	0	1	1	0	0	1	0	0	0
<i>F. tonerella</i>	1	0	0	0	2	0	0	0	0	0	0	0	0	1	1	0	0	1	0	0	0
<i>F. mediaseta</i>	1	0	0	0	1	0	0	0	0	6	0	0	0	1	1	0	0	1	0	0	0
<i>Pseudofabriciola australiensis</i>	2	0	0	1	3	2	1	0	0	0	0	1	0	3	1	0	0	1	0	0	0
<i>P. longa</i>	0	1	0	1	3	2	0	0	0	0	0	0	0	3	1	0	0	1	0	0	0
<i>P. incisura</i>	2	0	0	1	3	2	1	0	0	0	0	1	0	3	1	0	0	1	0	0	0
<i>P. capensis</i>	0	0	0	1	3	1	1	0	0	0	1	0	0	3	1	0	0	1	0	0	0
<i>P. filamentosa</i>	0	?	0	1	3	2	1	0	0	0	0	0	0	1	1	0	0	1	0	0	0
<i>P. californica</i>	0	0	0	1	3	1	0	0	0	0	1	0	0	2	1	0	0	1	0	0	0
<i>Fabricia stellaris</i>	0	0	0	0	4	0	0	0	0	4	1	0	0	1	1	0	0	1	0	0	0
<i>Augeneriella hummelincki</i>	3	0	0	0	4	0	0	0	0	3	1	0	0	1	1	0	0	1	0	0	0
<i>A. lagunari</i>	3	0	0	0	4	0	0	0	1	4	1	0	0	3	1	0	0	1	0	0	0
<i>A. pectinata</i>	3	0	0	0	4	0	0	0	0	3	1	0	0	3	1	0	0	1	0	0	0
<i>A. basifurcata</i>	3	0	0	0	4	0	0	0	1	4	1	0	0	3	1	0	0	1	0	0	0
<i>A. mossambica</i>	3	0	0	0	4	0	0	0	0	4	1	0	0	3	1	0	0	1	0	0	0
<i>Novafabricia chilensis</i>	0	1	0	0	5	0	0	0	0	3	1	0	1	3	1	0	0	1	0	0	0
<i>N. gerdi</i>	0	1	0	0	4	0	0	0	0	2	1	0	1	3	1	0	0	1	0	0	0
<i>N. infratorquata</i>	0	1	0	0	4	0	0	0	0	2	1	0	0	1	1	0	0	1	0	0	0
<i>N. triangularis</i>	0	1	0	0	4	0	0	0	0	2	1	0	0	2	1	0	0	1	0	0	0
<i>N. tenuiseta</i>	0	1	0	0	4	0	0	0	0	0	1	0	0	2	1	0	0	1	0	0	0
<i>Parafabricia ventricingulata</i>	0	0	0	0	4	0	0	0	0	4	1	0	0	3	1	0	0	1	0	0	0
<i>Fabricinuda limnicola</i>	2	2	0	0	6	0	0	1	0	5	1	0	0	3	1	0	0	1	0	0	0
<i>F. bikinii</i>	2	2	2	0	7	0	0	1	0	5	1	0	0	3	1	0	0	1	0	0	0
<i>F. trilobata</i>	2	2	1	0	7	0	0	1	0	5	1	0	0	3	1	0	0	1	0	0	0
<i>F. pseudocollaris</i>	2	2	0	0	7	0	0	1	0	5	1	0	0	3	1	0	0	1	0	0	0
<i>F. pseudopalpa</i>	0	0	0	0	7	0	0	1	0	5	1	0	0	3	1	0	0	1	0	0	0

(Monro, 1937), *P. filamentosa* (Day, 1963), *P. californica* Fitzhugh, 1991b, and *Augeneriella mossambica* (Day, 1957). Two additional *Manayunkia* species have been included, *M. baicalensis* and *M. polaris*, in an attempt to account for variability in branchial crown construction (see above) and thoracic inferior pseudospatulate setal distributions. Character states for these latter

two species were determined from the original descriptions.

Cladistic methods. — Minimum-length cladograms were constructed from the character state matrix (Table 2) using the commands **mhennig***; **bb*** of the program **Hennig86** (Farris 1988). All characters were given equal weight and multistate characters were treated as nonadditive. Character

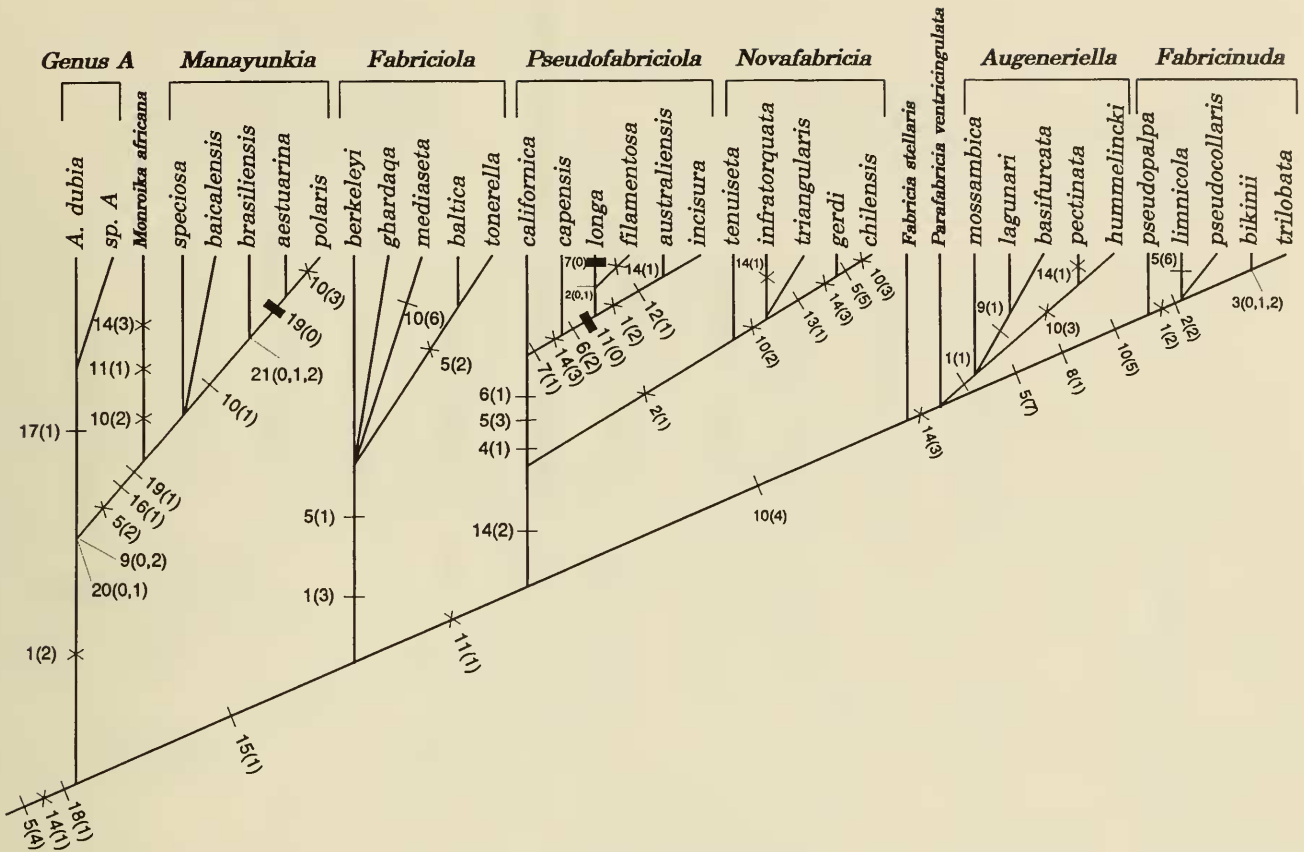


Fig. 5. One of 412 minimum-length cladograms for fabricioid taxa based on character-state distributions (Table 2), in which *Monroika* is a sister group to *Manayunkia*. Length is 60 steps, ci = 0.68, ri = 0.86. See Table 1 for explanations of character-state changes. Slashes on stems denote synapomorphies, X's are homoplasies, and black rectangles indicate reversals; ambiguous character-state assignments are indicated at the nodes.

consistency indices and character state transformation series on cladograms were determined from the *xsteps* command with the *h* and *c* options, respectively.

Results. — A total of 412 minimum-length cladograms were produced from the data matrix (Table 2), each with a length of 60 steps, a consistency index (ci) of 0.68, and a retention index (ri; Farris 1988, 1989) of 0.86.

In most respects, relationships at the generic level are consistent with results obtained by Fitzhugh (1991a, 1991b; e.g., Fig. 5). Topological ambiguity exists at this level with respect to two genera. In one case, *Fabriciola* is either the sister group of *Monroika* and *Manayunkia* (Fig. 6) by the presence of the membranous collar of the anterior peristomial ring [state 5(2)] or is the sister group to the clade containing *Fa-*

brica, *Augeneriella*, *Novafabricia* Fitzhugh, *Pseudofabriciola*, *Fabricinuda*, and *Parafabricia* (Fig. 5), defined by the presence of pygidial eyes [state 15(1)]. In the other situation, *Monroika* can be the sister taxon to *Manayunkia* (Figs. 5, 6) by the common presence of two pairs of radioles [state 16(1)] and displaced pinnules [state 19(1)], or else situated within *Manayunkia* (Figs. 7, 8) as either a sister group to species with pectinately arranged pinnules [state 21(0)] or a sister group to species with nonpectinate pinnules. The placement of *Monroika* as a sister group to *Manayunkia* is predicated on the ambiguous distribution of states for peristomial eyes (character 9) and shape of thoracic uncini (character 20).

In all cladograms, *Parafabricia* forms a trichotomy with *Augeneriella* and *Fabricinuda* (e.g., Fig. 5), this clade being defined

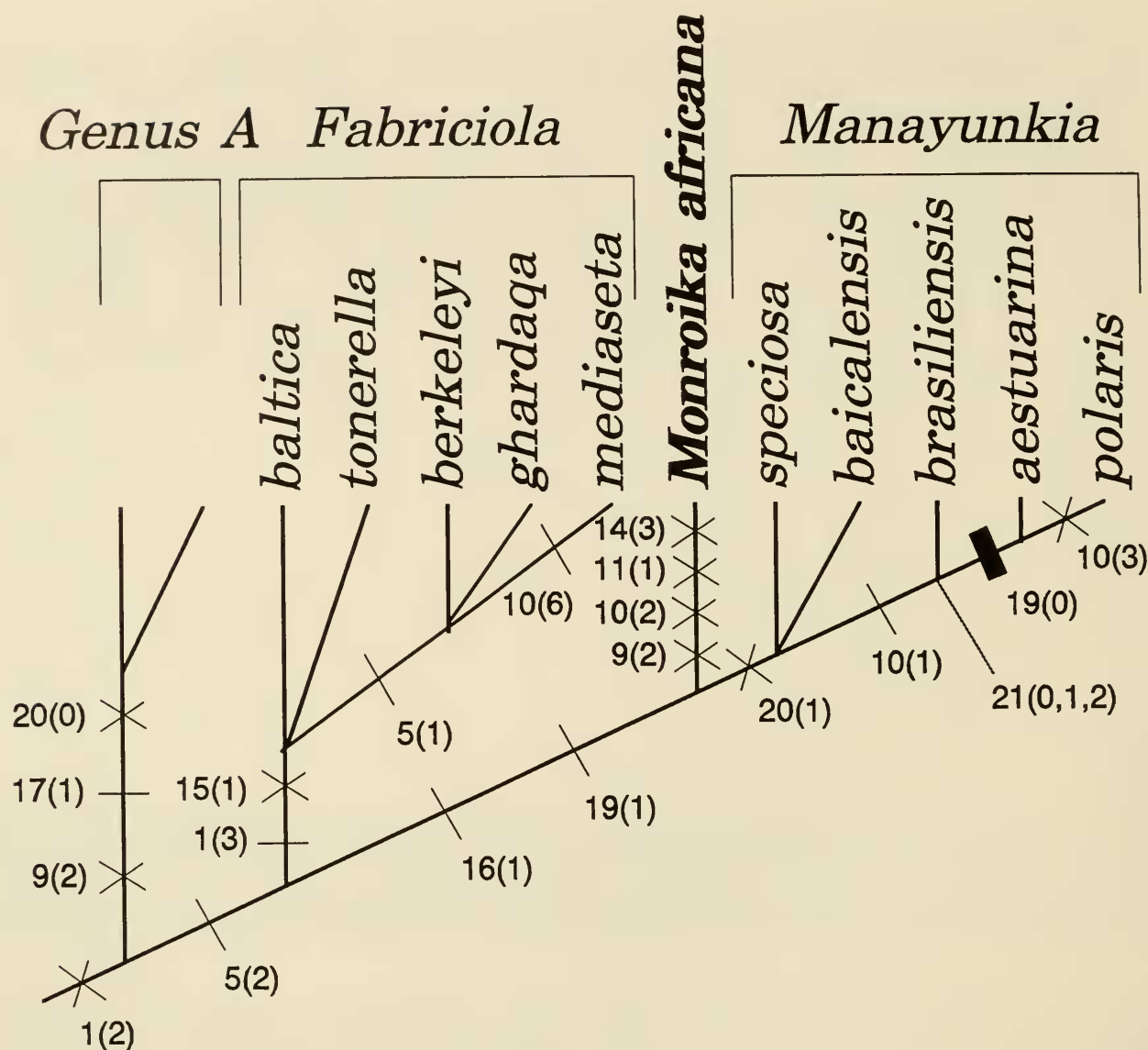


Fig. 6. A portion of a minimum-length cladogram for fabriciine taxa based on character-state distributions (Table 2), in which *Fabriciola* and *Monroika* are sister taxa to *Manayunkia*. Length is 60 steps, $ci = 0.68$, $ri = 0.86$. See Table 1 for explanations of character-state changes. All character-state changes are indicated; see Fig. 5 for explanations of symbols.

by the presence of abdominal uncini with a manubrium the same length as the dentate region [state 14(3)]. The sister group to this clade is *Fabricia*, represented here by *F. stellaris* Müller.

The large number of cladograms is primarily due to the numerous possible arrangements of species within *Manayunkia*, *Fabriciola*, *Novafabricia*, *Pseudofabriciola* and *Fabricinuda*. Patterns of ambiguity in the four latter genera are the same as reported by Fitzhugh (1991a, 1991b). Most notable for the present analysis is that there are 13 possible topologies for the placement

of *Monroika africana* within *Manayunkia* (Figs. 7, 8).

Discussion.—In light of the present results, two issues must be taken into consideration concerning the status of *Monroika*. First is the reliability of my interpretations of branchial crown characters. One might argue that until specimens in better condition are made available, it would be best to regard most branchial crown characters as unknown. I considered this alternative in an unpublished cladistic analysis in which most branchial crown characters (i.e., characters 1, 2, 16, 19) were coded as unknown

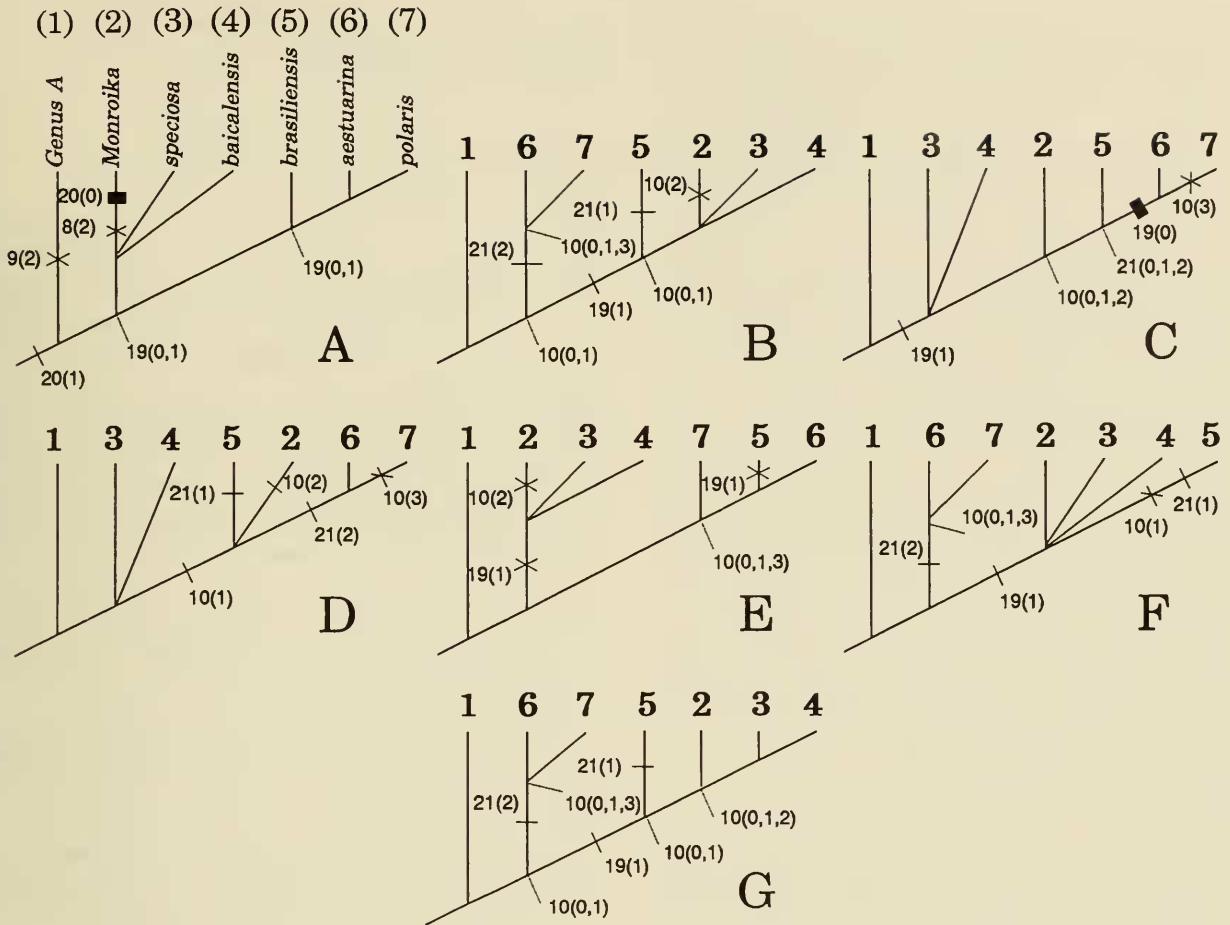


Fig. 7. Seven of 13 possible topologies (see also Fig. 8) among minimum-length cladograms in which *Monroika africana* is placed within the *Manayunkia* clade, based on character-state distributions (Table 2). Relationships among remaining taxa are the same as in Fig. 5. Character-state changes in A are the same as in Fig. 5 except where indicated; changes in B-G are the same as in A except where indicated. See Fig. 5 for explanations of symbols. Taxa in B-G are numbered as in A.

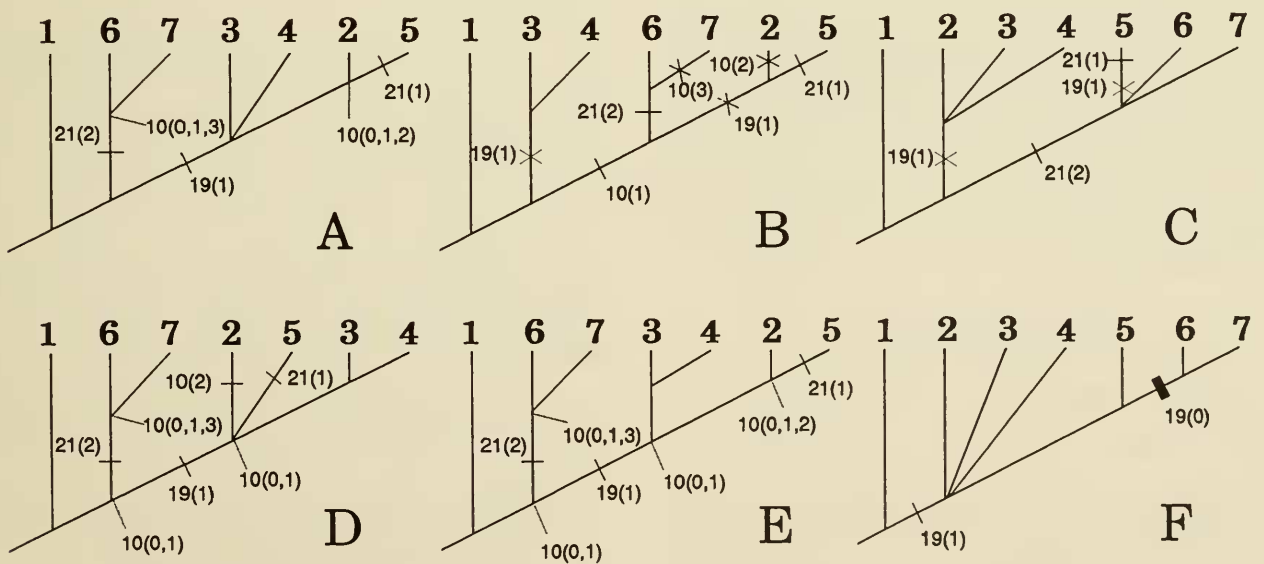


Fig. 8. Six of 13 possible topologies (see also Fig. 7) among minimum-length cladograms in which *Monroika africana* is placed within the *Manayunkia* clade, based on character-state distributions (Table 2). Relationships among remaining taxa are the same as in Fig. 5. Character-state changes are the same as in Fig. 7A except where indicated. Taxa are numbered as in Fig. 7A.

(="?""). All resulting cladograms (totaling over 1200) place *M. africana* out of the clade containing *Manayunkia* and Genus A (cf. Fig. 5) and into the clade containing *Fabricia*, *Novafabricia*, *Augeneriella*, *Fabricinuda*, and *Parafabricia*. Without the influence of these branchial crown characters, this alternative placement is allowed because of the nature of dentition in thoracic uncini (character 11), the distribution of thoracic inferior pseudospatulate setae (character 10), and condition of the manubrium of abdominal uncini (character 14). Since branchial crown characters play such an obvious role in determining the placement of *M. africana*, I am not at this time inclined to suggest placing this species back into *Manayunkia* though present character interpretations fully support such a move.

The second issue is the practicality of maintaining *Monroika* if *M. africana* is in fact a sister species to *Manayunkia* (e.g., Fig. 5). The general arguments for *Monroika* by Hartman (1951) and Jones (1974) are dependent upon the importance of recognizing levels of distinctness and the necessity of acknowledging taxonomic grades. Given the present results, maintaining *Monroika* would neither enhance nor harm the information content of sabellid systematics outside of creating redundancy by maintaining a near identical generic definition and type species diagnosis. If it is subsequently established that *M. africana* is a sister group to or occurs within *Manayunkia*, I would suggest placing this species back into its nominate genus.

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